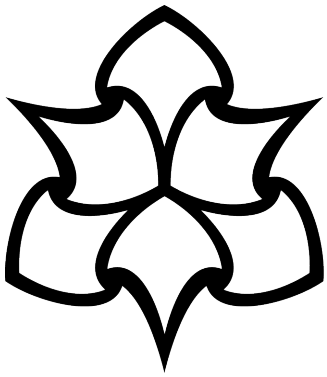

The ecology of the Asian dipterocarps

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The Dipterocarpaceae is the emblematic family of South-east Asian tropical rain forests and many of the seasonally dry forests of continental South and South-east Asia. Whilst dipterocarps are pantropical, with two sub-families Monotoideae and Pakaraimoideae found in Africa and South America (Maury-Lechon and Curtet 1998), Asian forests that can be dominated by dipterocarps occur from southern India throughout Malesia to New Guinea (Figures 1 and 2). In South-east Asia, the dominance of dipterocarps is evident in most mature forest communities, comprising around 20% of all trees (Slik et al. 2003) and a greater proportion of the larger forest trees; the majority are lowland species rarely found above 1200 m above sea level (Whitmore 1984). In the drier continental forests, dipterocarps make up a greater proportion of the trees but with reduced species diversity (Smitinand et al. 1980; Ashton 2014; Figure 2). Given this ecological predominance, advancing our knowledge of the ecology of dipterocarp species yields a better understanding of the forests of South and South-east Asia as a whole (Ashton 1988, 2014; Ghazoul 2016).

Dipterocarp trees are influential in the structure and function of Asian forests. They are amongst the tallest trees found in the tropics (Banin et al. 2012; Mongabay 2016a,b), making them important stores of above-ground carbon (Slik et al. 2013) and they are highly productive (Banin et al. 2014). These features, combined with their commercially favourable wood properties, clear straight boles and high stem density in accessible lowland forests meant they became widely

exploited for timber in the twentieth century (Sodhi et al. 2004). Indeed, many of the earliest studies of dipterocarps were by silviculturalists (e.g. Brandis 1895; Foxworthy 1932; Symington 1943). The forests of South-east Asia have therefore been shaped by a long management and disturbance history, with slightly less than half of the original forest area now remaining (Stibig et al. 2014). Whilst logging has declined in some parts of Asia, agriculture and the fragmentation associated with land conversion, pose further threats to the ecological functioning of remaining forest stands (Wilcove et al. 2013). Nonetheless, in recent years there has been an increased commitment to restoring forest cover in tropical Asia and new scientific understanding is required to determine how this might be done successfully (Chazdon 2008; Kettle 2010; Tuck et al. 2016). Evidently, forest restoration in much of Asia will have to rely on successful establishment of dipterocarp communities facilitated by a deeper understanding of their ecology.

The Asian dipterocarps are found in India (Antin et al. 2016), Bangladesh, Nepal, Sri Lanka and the Andaman Islands, in the seasonal forests of Thailand (Disyatat et al. 2016), Cambodia (Kenzo et al. 2016b), Vietnam (Dong et al. 2016 a, b; Nguyen and Baker 2016), Myanmar, Laos and into southern China. These drier forests are more open, shorter and have markedly lower diversity (Figures 1 and 2). Dipterocarps are found across Malesia, throughout the Malay peninsula (Chong et al. 2016; Kenzo et al. 2016a; Ng et al. 2016; Yamada et al. 2016), Sumatra, Java, and in Borneo (Ang et al. 2016; Brearley et al. 2016; Dent and Burslem 2016; Nutt et al. 2016; Saner et al. 2016) they reach their highest species diversity (Figure 2). East of Wallace's line, in neighbouring Sulawesi, diversity decreases markedly and although dipterocarp ranges extend to New Guinea (Figure 2), dipterocarp species constitute a much smaller component of the forest canopy.

The family-level dominance of the dipterocarps in the forests of South and South-east Asia has long fascinated ecologists; the closest tropical ecological equivalent are the stands of Caesalpinioideae subfamily of the Leguminosae found in west Africa and South America (Henkel 2003; Peh et al. 2011; Newbery et al. 2013). Dipterocarps have a number of ecological characteristics that all likely contribute, in some way, to their dominance, which play out at various points during

66 their life cycle (Figure 3). These include their non-pioneering yet often fast-growing
67 lifestyle (Thomas and Bazzaz 1999; Banin et al. 2014), mast fruiting (Ashton et al.
68 1988; Brearley et al. 2007; Numata et al. 2013), wind-dispersed winged fruits
69 (Suzuki and Ashton 1996; Smith et al. 2015) and symbiotic ectomycorrhizal
70 associations (Brearley 2011, 2012) (Figure 3). Under conditions relatively free from
71 exogenous disturbance, these family-wide traits and underlying mechanisms could
72 help dipterocarps gain a competitive advantage and lead to their ecosystem
73 dominance. Nonetheless, species within the family are certainly not equal and there
74 is clear variation in growth rates, wood density, maximum tree size, leaf form,
75 pollinators, seed size, dispersal distance, germination rates, and niche breadth
76 including edaphically- and irradiance-mediated habitat specialisation (Ashton
77 1964, 1982, 2014; Gunatilleke et al. 1997; Thomas and Bazzaz 1999; Marod et al.
78 2004; Russo et al. 2005; Philipson et al. 2012; O'Brien et al. 2013; Born et al. 2014;
79 Smith et al. 2015; Ghazoul 2016). Indeed, this functional variation and exploitation
80 of different environmental niches is one explanation for the maintenance of high
81 dipterocarp diversity, of over 500 species, in the tropical forests of Asia.
82
83 The key to understanding the ecology of the Asian dipterocarps lies in
84 improving our knowledge of the ecological processes at various scales, and the life-
85 cycle stage(s) at which these operate (Figure 3). This special issue compiles new
86 research relating to these key processes, across the majority of the Asian
87 dipterocarps' range. Ultimately, through understanding how dipterocarp species
88 reproduce, establish, function, and become organised in space and time, we can
89 better interpret the impacts of environmental change on the functioning, survival
90 and evolution of these communities and judge the effectiveness of management
91 interventions. Here, we briefly outline the key messages of the papers contained in
92 this special issue and conclude by placing the new understanding in the context of
93 the future for Asian forests.
94
95 ***Genetics and reproduction***
96 We have a reasonable picture of the broader branches of the dipterocarp phylogeny
97 with three subfamilies (Dipterocarpoideae, Monotoidae and Pakaraimoidae) and
98 two tribes (Dipterocarpeae and Shoreae) in the former subfamily (Dayanandan et

al. 1999; Gamage et al. 2006). This is confirmed by Ng et al. (2016) using two marker regions (*rpo*B and *trn*L). However, the 'twigs' of the tree, particularly within *Shorea* and closely related clades, still need attention – part of this lack of clarity is likely due to historical hybridisation events. Hybridisation between dipterocarp species is known (e.g. Kamiya et al. 2011) and may be one of the causes of high species diversity in this family. Kenzo et al. (2016a) examined a population of hybrid seedlings in Singapore and showed how their growth and survival rates are comparable to their parent species. However, the proportion of hybrids was greater at the seedling stage than the adult stage and they suggested that this might be due to increasing forest disturbance. At the population level, Ang et al. (2016) report that whilst naturally occurring seedlings of two dipterocarp species did not have lower genetic diversity in logged forest compared to unlogged forest, genetic variation within enrichment-planted seedlings was lower in monocultures compared to mixed-species plantings, presumably through post-planting mortality processes, which warrants further research. A possible mechanism for this was demonstrated by Nutt et al. (2016) who found *Parashorea tomentella* seedlings with greater heterozygosity had a greater survival rate, as did those with larger seeds, although neither seedling growth nor germination rate were influenced by heterozygosity. Ng et al. (2016) further fill a gap by providing new data on genome sizes for over 100 species of dipterocarps. Genome sizes were found to be consistently small (< 0.8 picograms in all cases). Because of the high nutrient demand for nucleic acids, it has been suggested that infertile soils, as found in much of South-east Asia (e.g. Banin et al. 2015), will lead to small genome sizes (Kang et al. 2015) supported by the data of Ng et al. (2016). However, there is still work to be done to determine the evolutionary importance and ecological correlates of genome size variation in dipterocarps and Ng et al. (2016) provides the starting point for this.

Dispersal and predation

Mast fruiting is hypothesised to be competitively advantageous to trees by satiating seed predators (Janzen 1974). Chong et al. (2016) studied the fates of seeds following a masting event at a fragmented site in Singapore to examine how human impacts on the forest might influence reproduction. Overall, they found that long-

tailed macaques were the dominant pre-dispersal seed predators whereas insects dominated predation post-dispersal. Vertebrate post-dispersal predation was more comparable to that of a logged forest than an intact forest in a previous study (Curran and Webb 2000), indicating possible changes in seed predation patterns associated with forest disturbance. Notably, Chong et al. (2016) identified a large proportion of non-viable seeds, which could be attributed to lower rates of out-crossing in a disturbed and fragmented landscape. Maintaining seed viability could become increasingly important for future dipterocarp communities, since it has also been established that successful reproduction may be lower in 'minor' masting events (Maycock et al. 2005) that appear to be increasing in frequency.

Leaf and stem traits

We are still learning how seedling ecophysiology drives species co-existence in dipterocarp communities, for example through the growth and survival strategies of light-demanding versus shade tolerant dipterocarps under resource-limited environmental conditions. Saner et al. (2016) observed six dipterocarp species and grouped the seedlings into light-demanding species that increased their growth rates after a simulated gap opening in contrast to shade tolerant species that showed a greater relative increase in non-structural carbohydrates. Although the role of non-structural carbohydrates in light adaptation is not well understood, it was found that enhanced non-structural carbohydrates were related to increased dipterocarp seedling drought survival in an earlier study (O'Brien et al. 2014). Kenzo et al. (2016b) looked at leaf traits of two common dipterocarps in dry deciduous dipterocarp forest in Cambodia and found strong relationships with height in the canopy. Canopy leaves had the fastest rate of photosynthesis - comparable to those in evergreen forests - despite a dry, hot and bright environment. These were maintained by thick leaves with a high nitrogen content and minimal stomatal limitation even in the early dry season. There were also clear seasonal differences with photosynthesis being faster in the wet season as stomata could remain open due to less water stress and, in general, the two species showed similar patterns in leaf ecophysiological traits, indicating their convergent adaptation to a highly seasonal environment. In contrast, Dent and Burslem (2016) showed differing leaf traits among saplings of nine dipterocarp species in a tropical

165 forest of Malaysian Borneo that had soil-specific edaphic preferences. Seedlings
166 specialised to more nutrient-poor sandy soil had strategies for nutrient and water
167 conservation such as lower foliar nitrogen and phosphorus concentrations, reduced
168 stomatal density and less negative $\delta^{13}C$, whereas those species specialised to more
169 nutrient-rich clay soils generally had traits with a broader range of values
170 (particularly for leaf mass per area and leaf lifespan). This has implications for the
171 high diversity of dipterocarps seen across Borneo as high alpha diversity on
172 nutrient-rich soils may be driven by a wider range of growth strategies (see also
173 Coomes et al. 2009) and the considerable edaphic variation leads to high beta
174 diversity across the island. Dong et al. (2016a) examined the ecophysiology of
175 *Hopea odorata* within artificial gaps in an *Acacia* plantation in a silvicultural
176 restoration experiment in Vietnam. They showed optimal physiological traits and
177 growth towards the centre of the gaps where irradiance was greatest; this species
178 demonstrated high phenotypic plasticity and rapid growth under high light
179 conditions indicating that it could be a good candidate for initial forest restoration.
180 In follow-up research, Dong et al. (2016b) showed that these seedlings achieved
181 such growth rates through a greater light-use efficiency, obtained by changes in
182 crown structure under the higher irradiance conditions. There was, however,
183 competition for water when growing near the gap edge and closer to the *Acacia*
184 nurse crop, suggesting consideration should be given to the choice of nurse crops to
185 minimise competitive interactions in restoration plantings (Dong et al. 2016a).
186 These studies indicate how information on species-level functioning can provide
187 insights for applied conservation and forest management, as well as fundamental
188 ecological understanding of factors influencing community assembly and diversity.
189
190 ***Mycorrhizas and soil processes***
191 Dipterocarps have long been known to be ectomycorrhizal (Singh 1966) with
192 ectomycorrhizas often credited as promoting faster growth rates and the high
193 species diversity and dominance of the family. Brearley et al. (2016) combined four
194 independent studies that manipulated connection to an ectomycorrhizal hyphal
195 network and found very little supporting evidence that this network influenced
196 seedling growth or survival over the short term. They hypothesised this was due to
197 low host specificity of ectomycorrhizal fungi meaning that there would be little

chance for adult trees to exclusively support kin through a hyphal network and it would not, therefore, provide an adaptive benefit. However, they did not actually examine the ectomycorrhizal fungi found in their study system, as did Disyatat et al. (2016); the latter looked at fungal diversity and composition in a dry dipterocarp forest fragment and a dipterocarp plantation in Thailand. They found lower ectomycorrhizal richness in the plantation and differences in ectomycorrhizal species composition between wet and dry seasons elucidating a previously overlooked temporal dimension to dipterocarp-associated ectomycorrhizal communities. Their traditional molecular research methods can be complemented in the future by using next generation sequencing for improving our understanding of tropical soil microbial processes (Peay et al. 2015; Thomas et al. 2015) and their links with their respective above-ground communities.

Structure and composition

Monitoring forest structure and composition has become increasingly important with a need to accurately and efficiently quantify carbon stocks and fluxes in association with REDD+ (Reducing Emissions from Deforestation and forest Degradation) policies (Miles and Kapos 2008). Changes in community composition may also alter the ability of a forest to sequester and store carbon. Thuy and Baker (2016) present a study on the dry dipterocarp forests of Vietnam based on numerous small sampling plots where four dipterocarp species made up about 80% of the trees. In terms of regeneration, the seedling composition in each plot was not always representative of the canopy composition and *Shorea siamensis* appeared to have poor regeneration capacity that is likely to lead to a changing species composition over time. Temporal forest dynamics were also explored by Antin et al. (2016) who used direct observations of diameter growth over a 21-year period in the Western Ghats of India, combined with allometric projections of height and crown dimensions to predict dynamics of the two dominant dipterocarps *Dipterocarpus indicus* and *Vateria indica*. They found that *Vateria indica* was a faster growing species in all dimensions in the majority of situations suggesting that it was increasing in dominance in the forest, possibly from some past disturbance. Yamada et al. (2016) examined the impacts of logging on five common dipterocarp species at Pasoh Forest Reserve in Peninsular Malaysia. An influence of past logging on tree

growth or mortality was not detected, but there was still a signature on patterns of recruitment that was an order of magnitude lower in logged forest, with the caveats that the study was based on only a single plot of each forest type and the logged plot may also have been impacted by edge effects. These studies indicate the need for monitoring a variety of structural parameters (horizontal and vertical), dynamic processes (growth, mortality and recruitment) and community members (adults, saplings and seedlings) to understand changes and predict the future of dipterocarp assemblages.

Disturbance and fragmentation

Forest disturbance and fragmentation are prevalent in the forests of South-east Asia (Sodhi et al. 2004; Wilcove et al. 2013) and understanding the impacts of these human-driven processes on dipterocarp-dominated forests is thus pressing. Numerous studies noted above addressed some aspects of forest disturbance or fragmentation. Ang et al. (2016) showed how logging had minimal impacts on seedling genetic diversity and Yamada et al. (2016) also found that logging did not impact tree growth rates or mortality but did influence recruitment. A number of studies used the small Bukit Timah Nature Reserve and surrounding secondary forest as examples of fragmented forest within an urbanised matrix (Corlett 1992) that may represent an extreme fate of dipterocarp forests in the future. Chong et al. (2016) indicated that fragmentation and disturbance might affect patterns of dipterocarp reproduction and successful seed dispersal and germination and Kenzo et al. (2016a) suggested that fragmentation may increase rates of hybridisaton. In a dry dipterocarp forest, Disyatat et al. (2016) further demonstrated that fragmentation can influence patterns of ectomycorrhizal fungal diversity. Varying results indicate both that different stages of the dipterocarp life cycle may be differentially affected by disturbance and fragmentation, and that the degree of disturbance and the environmental setting also play a role in determining tangible effects on dipterocarp communities.

Moving forward: applying autecological knowledge of dipterocarps to forest change, regeneration and restoration

The tropical forest biome is undergoing unprecedented environmental changes, including climatic, biogeochemical, fragmentation and extraction disturbances (Malhi et al. 2014). Particular challenges in South-east Asia include possible increasing frequency and/or intensity of El Niño-associated droughts and fires (e.g. Huijnen et al. 2016) and associated tree mortality (Slik 2004; Ngo et al. 2016) along with the widespread forest conversion to agriculture, forest fragmentation and associated edge effects and isolation effects. These landscape-level changes can alter forest biomass dynamics (Chaplin-Cramer et al. 2015), seedling performance (Yeong et al. 2016) and successful reproduction (Chong et al. 2016). Timber extraction has been extensive in the past, and long-lived taxa, such as the dipterocarps, may have a 'disturbance memory' of such perturbations, transcending generations and lasting decades or hundreds of years (e.g. Yamada et al. 2016). Understanding the fundamental ecology of this important taxon, and the processes that underpin the structure and function of dipterocarp communities will help us identify the ways in which Asian forests may be affected now and into the future.

Forest restoration is on the agenda in many Asian countries, with initiatives proposed or underway, for example, in Sabah, Malaysia (The Star 2015) and in India (Business Standard 2015). This is a welcome development and represents a distinct opportunity. Contributions to this special issue have demonstrated that successful regeneration and restoration programmes may require an understanding of the entire life cycle of target species and communities (see also Kettle 2010). Seed viability and seedling survival are affected by genetics of parent trees and their landscape context, in both natural regeneration and enrichment planting situations (Ang et al. 2016; Chong et al. 2016; Nutt et al. 2016; Kenzo 2016a). Seedling physiology, performance and competition in given environmental settings (Dent and Burslem 2016; Dong et al. 2016 a, b, Saner et al. 2016) and changes in communities over time through mortality and recruitment processes ultimately shape the future communities (Ang et al. 2016; Antin et al. 2016; Nguyen and Baker 2016). Perturbations to other biotic components (e.g. fungi, fauna) in these forest systems will also interact to affect rehabilitation of dipterocarp communities (Chong et al. 2016; Disyatat et al. 2016).

296 We acknowledge the challenge in knowledge transfer between those who
297 pursue fundamental research on the ecology of dipterocarps and those involved in
298 applied forest management. However, we hope that this special issue demonstrates
299 how bridges between fundamental research and applied questions can be crossed
300 and that the contributions within direct us to a new domain of confidence and a
301 more comprehensive understanding of the ecology of the Asian dipterocarps.
302
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310
311 **Notes on Contributors**
312 Francis Q. Brearley is an ecologist interested in the functional importance of plant-
313 soil interactions for ecological processes in tropical forests with a focus on the
314 dipterocarp-dominated forests of South-east Asia.
315 Lindsay F. Banin is a plant and ecosystem ecologist with a particular interest in
316 tropical forest systems and the impact of environmental changes on their function.
317 Philippe Saner is an environmental scientist with a main interest in tropical plant
318 community ecology and the restoration of tropical forests.
319
320 **References**
321 Ang CC, O'Brien M, Ng KKS, Lee PC, Hector A, Schmid B, Shimizu KK. 2016. Genetic diversity of two
322 tropical trees of the Dipterocarpaceae following logging and restoration in Borneo: high
323 genetic diversity in plots with high species diversity. Plant Ecology and Diversity XXX
324 Antin C, Le Bec J, Ayyappan N, Ramesh BR, Pélissier R. 2016. Allometric projections of time-related
325 growth trajectories of two co-existing dipterocarp canopy species in India. Plant Ecology and
326 Diversity XXX
327 Ashton PS. 1964. Ecological Studies in the Mixed Dipterocarp Forests of Brunei State, Oxford Forestry
328 Memoirs 25. Oxford (UK): Clarendon Press.
329 Ashton PS. 1982. Dipterocarpaceae. In: van Steenis CGGJ (editor). Flora Malesiana, Series 1,
330 Spermatophyta. The Hague (The Netherlands): Martinus Nijhoff Publishers, p. 237-552.

Ashton PS. 1988. Dipterocarp biology as a window to the understanding of tropical forest structure. Annual Review of Ecology and Systematics 19:347-370.

Ashton PS. 2014. On the Forests of Tropical Asia: Lest the Memory Fade. London (UK): Royal Botanic Gardens, Kew.

Ashton PS, Givnish TJ, Appanah S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. The American Naturalist 132:44-66.

Banin L, Feldpausch TR, Phillips OL, Baker TR, Lloyd J, Affum-Baffoe K, Arets EJMM, Berry NJ, Bradford M, Brienen RJW, Davies S, Drescher M, Higuchi N, Hilbert DW, Hladik A, Iida Y, Abu Salim K, Kassim AR, King DA, Lopez-Gonzalez G, Metcalfe D, Nilus R, Peh KS-H, Reitsma JM, Sonké B, Taedoumg H, Tan S, White L, Wöll, Lewis SL. 2012. What controls tropical forest architecture? Testing environmental, structural and floristic drivers. Global Ecology and Biogeography 21:1179-1190.

Banin L, Lewis SL, Lopez-Gonzalez G, Baker TR, Quesada CA, Chao K-J, Burslem DFRP, Nilus R, Abu Salim K, Keeling HC, Tan S, Davies SJ, Monteagudo Mendoza A, Vásquez R, Lloyd J, Neill DA, Pitman N, Phillips OL. 2014. Tropical forest wood production: a cross-continental comparison. Journal of Ecology 102:1025-1037.

Banin LF, Phillips OL, Lewis SL. 2015. Tropical forests. In: Peh KS-H, Corlett RT, Bergeron Y (editors). Routledge Handbook of Forest Ecology. Abingdon (UK): Routledge. p. 56-75.

Born J, Pluess AR, Burslem DFRP, Nilus R, Maycock C, Ghazoul J. 2014. Differing life history characteristics support coexistence of tree soil generalist and specialist species in tropical rain forests. Biotropica 46:58–68.

Brandis D. 1895. An enumeration of the *Dipterocarpaceæ*, based chiefly upon the specimens preserved at the Royal Herbarium and Museum, Kew, and the British Museum; with remarks on the genera and species. Journal of the Linnean Society 31:1-148.

Brearley FQ. 2011. The importance of ectomycorrhizas for the growth of dipterocarps and the efficacy of ectomycorrhizal inoculation schemes. In: Rai M, Varma A (editors). Diversity and Biotechnology of Ectomycorrhizae. Berlin (Germany): Springer-Verlag. p. 3-17.

Brearley FQ. 2012. Ectomycorrhizal associations of the Dipterocarpaceae. Biotropica 44:637-648.

Brearley FQ, Proctor J, Nagy L, Dalrymple G, Suriantata, Voysey BC. 2007. Reproductive phenology over a 10-year period in a lowland evergreen rain forest of central Borneo. Journal of Ecology 95: 828–839.

Brearley FQ, Saner P, Uchida A, Burslem DFRP, Hector A, Nilus R, Scholes JD, Egli S. 2016. Testing the importance of a common ectomycorrhizal network for dipterocarp seedling growth and survival in tropical forests of Borneo. Plant Ecology and Diversity XXX

Business Standard. 2016. CAF Bill will help increase country's forest cover to 33 per cent. http://www.business-standard.com/article/pti-stories/caf-bill-will-help-increase-country-s-forest-cover-to-33-per-116050301458_1.html [Accessed 1 December 2016]

Chaplin-Kramer R, Ramler I, Sharp R, Haddad NM, Gerber JS, West PC, Mandle L, Engstrom P, Baccini A, Sim S, Mueller C, King H. 2015. Degradation in carbon stocks near tropical forest edges. Nature Communications. 6:10158.

Chazdon RL. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320:1458-1460.

Chong KY, Chong R, Tan LWA, Yee ATK, Chua MAH, Wong KM, Tan HTW. 2016. Seed production and survival of four dipterocarp species in degraded forests in Singapore. Plant Ecology and Diversity XXX

Coomes DA, Kunstler G, Canham CD, Wright E. 2009. A greater range of shade-tolerance niches in nutrient-rich forests: an explanation for positive richness–productivity relationships? Journal of Ecology 97: 705–717.

Corlett RT. 1992. The ecological transformation of Singapore, 1819-1990. Journal of Biogeography 19:411-420.

Curran LM, Webb CO 2000. Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. Ecological Monographs 70:129-148.

Dayanandan S, Ashton PS, Williams SM, Primack RB. 1999. Phylogeny of the tropical tree family Dipterocarpaceae based on nucleotide sequences of the chloroplast *rbcL* gene. American Journal of Botany, 86:1182-1190.

Dent DH, Burslem DFRP. 2016. Leaf traits of dipterocarp species with contrasting distributions across a nutrient and light availability gradient. Plant Ecology and Diversity XXX

Disyatat NR, Yomyart S, Sihanonth P, Piapukiew J. 2016. Community structure and dynamics of ectomycorrhizal fungi in a dipterocarp forest fragment and plantation in Thailand. Plant Ecology and Diversity XXX

Dong TL, Beadle C, Eyles A, Forrester DI, Doyle R, Worledge D, Churchill K, Khanh DC. 2016a. Growth and physiology of *Hopea odorata* planted within gaps in an acacia plantation acting as a nurse crop. Plant Ecology and Diversity XXX

Dong TL, Forrester DI, Beadle C, Doyle R, Hoang NH, Giap NX, Worledge D. 2016b. Effects of light availability on crown structure, biomass production, light absorption and light-use efficiency of *Hopea odorata* planted within gaps in *Acacia* hybrid plantation. Plant Ecology and Diversity XXX

Foxworthy FW. 1932. Dipterocarpaceae of the Malay Peninsula. Kuala Lumpur (Malaya): Federated Malay States Government.

Gamage DT, de Silva MP, Inomata N, Yamazaki T, Szmidt AE. 2006. Comprehensive molecular phylogeny of the sub-family Dipterocarpoideae (Dipterocarpaceae) based on chloroplast DNA sequences. Genes and Genetic Systems 81:1-12.

Ghazoul J. 2016. Dipterocarp Biology, Ecology, and Conservation. Oxford (UK): Oxford University Press.

Gunatilleke CVS, Gunatilleke IAUN, Perera GAD, Burslem DFRP, Ashton PMS, Ashton PS. 1997. Responses to nutrient addition among seedlings of eight closely related species of *Shorea* in Sri Lanka. Journal of Ecology 85:301-311.

409 Henkel TW. 2003. Monodominance in the ectomycorrhizal *Dicymbe corymbosa* (Caesalpiniaceae)
410 from Guyana. Journal of Tropical Ecology 19:417-437.
411 Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate
412 surfaces for global land areas. International Journal of Climatology 25:1965-1978.
413 Huijnen V, Wooster MJ, Kaiser JW, Gaveau DLA, Flemming J, Parrington M, Inness A, Murdiyarso D,
414 Main B, van Weele M. 2016. Fire carbon emissions over maritime Southeast Asia in 2015
415 largest since 1997. Scientific Reports 6:26886.
416 Jacobs M. 1981. Dipterocarpaceae, the taxonomic and distributional framework. Malaysian Forester
417 44:168-189.
418 Janzen DH. 1974. Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae.
419 Biotropica 6:69-103.
420 Kamiya K, Gan YY, Lum SKY, Khoo MS, Chua SC, Faizu NNH. 2011. Morphological and molecular
421 evidence of natural hybridization in *Shorea* (Dipterocarpaceae). Tree Genetics and Genomes
422 7:297-306.
423 Kang M, Wang J, Huang H. 2015. Nitrogen limitation as a driver of genome size evolution in a group
424 of karst plants. Scientific Reports 5:11636.
425 Kenzo T, Ichie T, Norichika Y, Kamiya K, Nanami S, Igarashi S, Sano M, Yoneda R, Lum SKY. (2016a)
426 Growth and survival of hybrid dipterocarp seedlings in a tropical rain forest fragment in
427 Singapore. Plant Ecology and Diversity XXX
428 Kenzo T, Iida S, Shimizu T, Tamai K, Kabeya N, Shimizu A, Chann S. (2016b) Seasonal and height-
429 related changes in leaf morphological and photosynthetic traits of two dipterocarp species in
430 a dry deciduous forest in Cambodia. Plant Ecology and Diversity XXX
431 Kettle CJ. 2010. Ecological considerations for using dipterocarps for restoration of lowland rainforest
432 forests in Southeast Asia. Biodiversity and Conservation 19:1137-1151.
433 Li XW, Li J, Ashton PS. 2000. Dipterocarpaceae. In: Wu ZY, Raven PH, Hong DY (editors]. Flora of
434 China, Volume 13. (Beijing, China) Science Press & (St Louis, USA) Missouri Botanical Garden
435 Press. p. 48-54.
436 Malhi Y, Gardner TA, Goldsmith GR, Silman MR, Zelazowski P. 2014. Tropical Forests in the
437 Anthropocene. Annual Review of Environment and Resources 39:125-159.
438 Marod D, Kutintara U, Tanaka H, Nakashizuka T. 2004. Effects of drought and fire on seedling survival
439 and growth under contrasting light conditions in a seasonal tropical forest. Journal of
440 Vegetation Science 15:691-700.
441 Maury-Lechon G, Curtet L. 1998. Biogeography and evolutionary systematics of Dipterocarpaceae.
442 In: Appanah S, Turnbull JM (editors) A Review of Dipterocarps: Taxonomy, Ecology and
443 Silviculture. Bogor (Indonesia): Center for International Forestry Research. p. 5-44.
444 Maycock CR, Thewlis RN, Ghazoul J, Nilus R, Burslem DFRP. 2005. Reproduction of dipterocarps
445 during low intensity masting events in a Bornean rain forest. Journal of Vegetation Science
446 16:635-646.
447 Miles L, Kapos V. 2008. Reducing greenhouse gas emissions from deforestation and forest
448 degradation: global land-use implications. Science 320:1454-1455.

449 Mongabay. 2016a. Tropics' tallest tree found in Malaysia.
450 https://news.mongabay.com/2016/06/tropics-tallest-tree-found-in-malaysia/ [Accessed 24
451 November 2016]
452 Mongabay. 2016b. World's tallest tropical tree discovered, along with nearly 50 other record-
453 breakers. https://news.mongabay.com/2016/11/worlds-tallest-tropical-tree-discovered-
454 along-with-nearly-50-other-record-breakers/ [Accessed 24 November 2016]
455 Newbery DM, van der Burgt XM, Worbes M, Chuyong GB. 2013. Transient dominance in a central
456 African rain forest. Ecological Monographs 83:339-382.
457 Ng CH, Lee SL, Tnah LH, Ng KKS, Lee CT, Madon M. 2016. Genome size variation and evolution in
458 Dipterocarpaceae. Plant Ecology and Diversity XXX
459 Ngo KM, Davies S, Hassan NFN, Lum S. 2016. Resilience of a forest fragment exposed to long-term
460 isolation in Singapore. Plant Ecology and Diversity XXX
461 Nguyen TT, Baker PJ. 2016. Structure and composition of deciduous dipterocarp forest in Central
462 Vietnam: patterns of species dominance and regeneration failure. Plant Ecology and Diversity
463 XXX
464 Numata S, Yasuda M, Suzuki RO, Hosaka T, Noor NSM, Fletcher CD, Hashim M. 2013. Geographical
465 pattern and environmental correlates of regional-scale general flowering in Peninsular
466 Malaysia. PloS One 8:e79095.
467 Nutt KS, Burslem DFRP, Maycock CR, Ghazoul J, Khoo E, Hastie A, Kettle CJ. 2016. Genetic diversity
468 affects seedling survival but not growth or seed germination in the Bornean endemic
469 dipterocarp *Parashorea tomentella*. Plant Ecology and Diversity XXX
470 O'Brien MJ, Philipson CD, Tay J, Hector A. 2013. The influence of variable rainfall frequency on
471 germination and early growth of shade-tolerant dipterocarp seedlings in Borneo. PLoS One
472 8:e70287.
473 O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014. Drought survival of tropical tree seedings
474 enhanced by non-structural carbohydrate levels. Nature Climate Change 4:710-714.
475 Peay KG, Russo SE, McGuire KL, Lim Z, Chan JP, Tan S, Davies SJ. 2015. Lack of host specificity leads
476 to independent assortment of dipterocarps and ectomycorrhizal fungi across a soil fertility
477 gradient. Ecology Letters 18:807-816.
478 Peh KS-H, Lewis SL, Lloyd J. 2011. Mechanisms of monodominance in diverse tropical tree-
479 dominated systems. Journal of Ecology 99:891-898.
480 Philipson CD, Saner P, Marthews TR, Nilus R, Reynolds G, Turnbull LA, Hector A. 2012. Light-based
481 regeneration niches: evidence from 21 dipterocarp species using size-specific RGRs.
482 Biotropica. 44:627–636.
483 Russo SE, Davies SJ, King DA, Tan S. 2005. Soil-related performance variation and distributions of
484 tree species in a Bornean rain forest. Journal of Ecology 93:879-889.
485 Saner P, Philipson CD, Peters S, Keller F, Bigler L, Turnbull LA, Hector A. 2016. Growth rates and
486 relative change in non-structural carbohydrates of dipterocarp seedlings in response to light
487 acclimation. Plant Ecology and Diversity XXX

488 Singh, KG. 1966. Ectotrophic mycorrhiza in equatorial rain forests. Malayan Forester 29:13-18.
489 Slik JWF. 2004. El Niño droughts and their effects on tree species composition and diversity in
490 tropical rain forests. Oecologia 141:114-120.
491 Slik JWF, Poulsen AD, Ashton PS, Cannon CH, Eichhorn KAO, Kartawinata K, Lanniari I, Nagamasu H,
492 Nakagawa M, van Nieuwstadt MGL, Payne J, Purwaningsih, Saridan A, Sidiyasa K, Verburg RW,
493 Webb CO, Wilkie P. 2003. A floristic analysis of the lowland dipterocarp forests of Borneo.
494 Journal of Biogeography 30:1517-1531.
495 Slik JWF, Paoli G, McGuire K, Amaral I, Barroso J, Bastian M, Blanc L, Bongers F, Boundja P, Clark C,
496 Collins M, Dauby G, Ding Y, Doucet J-L, Eler E, Ferreira L, Forshed O, Fredriksson G, Gillet J-F,
497 Harris D, Leal M, Laumonier Y, Malhi Y, Mansor A, Martin E, Miyamoto K, Araujo- Murakami A,
498 Nagamasu H, Nilus R, Nurtjahya E, Oliveira A, Onrizal O, Parada-Gutierrez A, Permana A,
499 Poorter L, Poulsen J, Ramirez-Angulo H, Reitsma J, Rovero F, Rozak A, Sheil D, Silva-Espejo J,
500 Silveira M, Spironelo W, ter Steege H, Stevart T, Navarro-Aguilar GE, Sunderland T, Suzuki E,
501 Tang J, Theilade I, van der Heijden G, van Valkenburg J, Do TV, Vilanova E, Vos V, Wich S, Wöll
502 H, Yoneda T, Zang R, Zhang M-G, Zweifel N. 2013. Large trees drive forest aboveground
503 biomass variation in moist lowland forests across the tropics. Global Ecology and
504 Biogeography 22:1261-1271.
505 Smitinand T, Santisuk T, Phengklai C. 1980. The manual of Dipterocarpaceae of mainland South-East
506 Asia. Thai Forest Bulletin (Botany) 12:1-133.
507 Smith J, Bagchi R, Ellens J, Kettle CJ, Burslem DFRP, Maycock CR, Khoo E, Ghazoul J. 2015. Predicting
508 dispersal of auto-gyrating fruit in tropical trees: a case study from the Dipterocarpaceae.
509 Ecology and Evolution 5:1794-1801.
510 Sodhi NS, Koh LP, Brock BW, Ng PKL. 2004 Southeast Asian biodiversity: an impending disaster.
511 Trends in Ecology and Evolution 19:654-660.
512 The Star. 2015. Sabah to restore 200,000ha of degraded forests.
513 http://www.thestar.com.my/news/nation/2015/06/30/sabah-to-restore-200000ha-of-
514 degraded-forests/ [Accessed 30November 2016]
515 Stibig H-J, Achard F, Carboni S, Raši R, Miettinen J. 2014. Change in tropical forest cover of Southeast
516 Asia from 1990 to 2010. Biogeosciences 11:247-258.
517 Suzuki E, Ashton PS. 1996. Sepal and nut size ratio of fruits of Asian Dipterocarpaceae and its
518 implications for dispersal. Journal of Tropical Ecology 12:853-870.
519 Symington CF. 1943. Foresters' Manual of Dipterocarps. Kuala Lumpur (Malaysia): Penerbit
520 Universiti Malaya.
521 Thomas AD, Corre MD, Schwendenmann L, Veldkamp E, Fujii K, Mkwambisi D, McGuire KL, Ng
522 Cheong R, Powers JS, Brearley FQ. 2015. Soils and land-use change in tropical and savannah
523 environments: emerging themes and future research directions. In: Brearley FQ, Thomas AD
524 (editors). Land-Use Change Impacts on Soil Processes: Tropical and Savannah Environments.
525 Wallingford (UK): CABI, p. 176-181.
526 Thomas SC, Bazzaz FA. 1999. Asymptotic height as a predictor of photosynthetic characteristics in
527 Malaysian rain forest trees. Ecology 80:1607-1622.

528 Tuck SL, O'Brien MJ, Philipson CD, Saner P, Tanadini M, Dzulkifli D, Godfray HCJ, Godoong E, Nilus R,
529 Ong RC, Schmid B, Sinun W, Snaddon JL, Snoep M, Tangki H, Tay J, Ulok P, Yap SW,
530 Weilenmann M, Reynolds G, Hector A. 2016. The value of biodiversity for the functioning of
531 tropical forests: insurance effects during the first decade of the Sabah Biodiversity
532 Experiment. Proceedings of the Royal Society of London B:20161451.
533 Whitmore TC. 1984. Tropical Rain Forests of the Far East, 2nd Edition. Oxford (UK): Clarendon Press.
534 Wilcove DS, Giam X, Edwards DP, Fisher B, Koh LP. 2013. Navjot's nightmare revisited: logging,
535 agriculture, and biodiversity in Southeast Asia. Trends in Ecology and Evolution 28:531-540.
536 Yamada, T, Moriwaki Y, Okuda T, Kassim AR. 2016. Long-term effects of selective logging on
537 dipterocarp populations in the Pasoh Forest Reserve, Malaysia. Plant Ecology and Diversity
538 XXX
539 Yeong KL, Reynolds G, Hill JK. 2016. Enrichment planting to improve habitat quality and conservation
540 value of tropical rainforest fragments. Biodiversity and Conservation 25:957-973.

Figure 1: Dipterocarp-dominated forest types in South and South-east Asia including some of the study sites in this special issue. Dry dipterocarp forest in Kratie province (Cambodia) in the (a) wet season and (b) dry season; (c) Lowland evergreen rain forest at Gunung Mulu, Sarawak, northern Borneo; (d) Heath forest (also known as *kerangas*) at Barito Ulu, central Borneo; (e) Bukit Timah, a fragment of dipterocarp forest in Singapore; (f) canopy walkway at Pasoh Forest Reserve, Peninsular Malaysia; (g) Uppangala in the Western Ghats of India; (h) Danum Valley in Sabah, northern Borneo; (i) forest in Murung Raya regency, central Borneo showing traversing logging road. Photos by Tanaka Kenzo (a, b, e), Lindsay Banin (c), Francis Brearley (d, f, i), Jimmy Le Bec (g) and Ch'ien Lee (h).

Figure 2: Map of South and South-east Asia depicting mean annual precipitation across the region (from WORLDCLIM; Hijmans et al. 2005) with region-specific species richness values for members of the Dipterocarpaceae. Species richness data come from Ashton (1982) for Peninsular Malaysia, Sumatra, Java, Borneo, The Philippines, Sulawesi and New Guinea, Jacobs (1981) for Sri Lanka, Thailand, Cambodia and Vietnam and Li et al. (2000) for Chin). Photos by Aswandi (Sumatra), Shangwen Xia (China), Thuy Nguyen Thi (Vietnam) and Liam Trethowan (Sulawesi).

Figure 3: Key stages of the dipterocarp life cycle (inner circle) and the linkages with fundamental environmental processes (symbols on outer circle) that are discussed in this special issue. Note that the ecological processes cannot be linked to a single life cycle stage, but represent the approximate scale at which the process operates and/or the starting point for interaction among stages and processes through the life cycle. © Diogo Guerra.